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triple allelomorphism. For this reason I am inclined to assign priority to Morgan and Lynch,[9] whose paper on linkage of genes in *Drosophila* which are not sex-linked appeared after my own paper and before Punnett's.

COLUMBIA UNIVERSITY A. H. STURTEVANT

NABOURS'S BREEDING EXPERIMENTS WITH GRASSHOPPERS

IN a recent paper, Nabours ('14) describes breeding experiments that he has been carrying on for some years with grouse locusts of the genus *Paratettix*. His work is of special interest in showing that in a wild species there exists a number of distinct types that show alternative inheritance of a particular kind. His paper may be summarized as follows:

1. Nine distinct, true breeding forms of *Paratettix* were collected "in nature." These "species" (as Nabours is inclined to consider them) "are mainly distinguished by their striking color patterns."
2. When an individual of one of these species is mated to one of a different species the hybrid character of the offspring is apparent at once, in that "all the characters of each parent are represented in the F_1 hybrid." In other words, the hybrid is in a certain sense an intermediate, and "the terms dominant and recessive" are probably not "applicable at all." This point, while of little theoretic importance, has a practical value in that the zygotic constitution of any hybrid can be recognized without further breeding tests.
3. With one exception, each color pattern factor was found to behave as an allelomorph to any other color pattern factor.
4. The various lengths of the wings and pronotum are apparently not inherited, as such but are determined by environmental factors, especially such as tend to prolong or to shorten the length of larval life.

It appears that Nabours confuses the relation of the facts mentioned under 3, and that he supposes this to be the ordinary behavior of "mendelizing characters," for he says:

> The essential result of these experiments has been the extension of this principle [Mendelian inheritance] to a considerable number of types of a phylogenetically low group of ametabolous insects.

To be sure, he recognizes that other workers in genetics have an attitude quite different from his, and he takes some little pains to make clear his own point of view. To quote again (p. 142):

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[9] *Biol. Bull.*, XXIII, 1912 (Aug.).

> The existence of unit characters in the De Vriesian sense does not appear to have been as clearly demonstrated as that of alternative inheritance . . . and the interpretations are at great variance. Thus, one group of authors [reference made to Bateson, Doncaster, and Tower] recognize characters in organisms that can be replaced by other characters when the proper crosses are made, . . . while on the other side there are those [references to Whitman and Montgomery] who believe that the organism as a whole is the only unit and that there are no actual unit characters.

Again he says (p. 169):

> No character of one parent species is ever replaced in the F_1 hybrid by any character of the other parent. All the characters of each parent are represented in the F_1 hybrid. It follows then that these grasshoppers do not exhibit characters which by crossing can be replaced by other different characters; the whole pattern appears to be the only unit.

There is no real conflict between Whitman's idea and the accounts given by students of Mendelism, for the latter realize that far-reaching somatic effects may result from a single factor, and the composite character of the hybrid is not an uncommon occurrence. Nabours identifies a particular pattern with the "organism as a whole," but since his evidence relates here to color patterns only, nothing is gained by the introduction of such a vague phrase as the "organism as a whole." Specifically he shows that the hereditary differences between any two types can be explained on the assumption of a single differential for each case.

With reference to the antithesis presented by Nabours, it must be recognized that the modern literature of Mendelian heredity affords innumerable instances where two or more characters entering from one parent and their allelomorphs from the other, reappear in the F_2 generation in new combinations.

If we assume with Nabours that each of the eight color patterns are represented by a characteristic condition of the "germinal material," we may use his terms *A, B, C, D, E, F, H* or *I* to symbolize this "germinal material" for the various color patterns. As Nabours uses the terms, an individual homozygous for *A* is represented simply by *A,* and a hybrid between *A* and *B* by *AB*. In ordinary usage, the homozygous form would be represented as *AA* and its germ cells by *A*. This is a minor matter. Ordinary usage has the advantage of being more consistent.

According to Nabours, then, *A* mated to *B* gives *AB; B* mated to *F* gives *BF; C* mated to *E* gives *CE,* etc. In gametogenesis these factors segregate, so that, for example, *BA* gives germ cells

A and *B; BF* gives *B* and *F,* etc. In other words, he treats the matter as if he were dealing with a system of multiple allelomorphs, though he nowhere specifically calls them such. From this point of view there are eight distinct allelomorphs concerned with color pattern any two of which may constitute a pair; in any zygote two allelomorphs (perhaps alike, perhaps unlike) will be present, and in any gamete only one of the eight will normally occur.

With one exception of which I will treat later, all of Nabours's results can be explained by this hypothesis. This sort of explanation is not new. (Shull ('11), de Meijere ('10), Sturtevant ('13) and others have used it to explain results obtained in *Lychnis, Papilio,* rabbits and other forms, and it will almost undoubtedly be shown to apply satisfactorily in still other cases.

The exception just mentioned occurred in the cross which Nabours describes at the bottom of page 156 (*e*). Here a male of the constitution *CE* was mated to a female of the constitution *BI.* On Nabours's theory, the gametes of the male should carry *C* or *E,* but not both, and the gametes of the female should carry *B* or *I,* but not both. The union of the two kinds of sperms with the two kinds of eggs should give four classes of offspring, and these were in fact obtained; viz., 12 *BC,* 11 *BE,* 7 *CI,* 10 *EI.* But there appeared also one individual *BEI.* Nabours's explanation of the case is that perhaps the *BI* "female parent gave at least one gamete containing the factors for the patterns of both her parents and that this double character gamete was fertilized by one of the *E* gametes which came from the *CE* male."[1] Let us see whether this is the most probable interpretation.

As Sturtevant has pointed out, for any case to which the idea of multiple allelomorphism is applicable, an equally valid explanation may be found in "complete linkage" of the factors concerned. To decide in any case between the two explanations would be impossible.

If, however, linkage were not complete, a "cross-over" class or "recombination" class might occur, and this would suffice to rule out the explanation based on multiple allelomorphs.

Such a "cross-over" class perhaps is furnished by the *BEI* individual. The demonstration of this may be given by the use of symbols, as follows:

Let us assume that *A* is the allelomorph of *a, B* that of *b, C* of *c, D* of *d, F* of *f, I* of *i,* etc., making eight pairs of allelomorphs altogether. Assume that each gamete of any individual carries one allelomorph of each pair, and that the eight factors thus present in a gamete form a linked group, tending to segregate as a unit in gametogenesis. Thus Nabours's form *A* would give gametes of the form *Abcdefhi*. *AB* would give gametes of only two forms, one corresponding to *A* and the other to *B*, viz., *Abcdefhi* and *aBcdefhi*. Two other forms are possible, formed by the exchange of *A* with *B*, and of *a* with *b*, but these will not occur if linkage is complete. In dealing with the hybrid *AB* in practise the factors *cdefhi* would not be put into the formulæ, as they are alike in all gametes.

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[1] This explanation is essentially similar to that advanced by Bridges ('13) to explain certain peculiar results in *Drosophila.* Bridges assumed that in gametogenesis the two X-chromosomes of a white-eyed female failed to segregate (in Bridge's terminology, non-disjunction occurred), and passed over together into one gamete.

These rules would apply similarly to all other species and hybrids. Therefore in the case in which the *BEI* individual occurred, we would represent the male parent, which Nabours designated *CE*, by *bCei–bcEi*, and its gametes by *bCei* and *bcEi*. The female parent, which Nabours designates *BI*, we would represent by *Bcei–bceI*, and its gametes would be *Bcei* and *bceI* if linkage were complete. If linkage were not complete there would occasionally be formed gametes *bcei* and *BceI*. One of these latter (*BceI*) was probably formed and fertilized by a sperm of the type *bcEi*, thus giving rise to the *BEI* individual. No gametes corresponding to *bcei* appear to have been fertilized, though of course we do not yet know what the appearance would be of an individual so formed.

This matter would be easy to test, and it is to be hoped the cross may be repeated. If then *BEI* forms should appear again and in these when mated to other forms the factors B and I should be found to stay together to the same extent as they before separated, it would show that close linkage, rather than multiple allelomorphism explains this particular instance.

It may be, too, that both linkage and multiple allelomorphism play a part in the production of these phenomena. In any case it seems that the test is at hand, and not difficult to perform, excepting in so far as there are practical difficulties connected with the rearing of the grasshoppers in sufficient numbers to cover the point.

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COLUMBIA UNIVERSITY JOHN S. DEXTER